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Comparative Photosynthetic Capacity of Abaxial and Adaxial Leaf Sides as Related to Exposure in Two Epiphytic Ferns in a Subtropical Rainforest in Northeastern Taiwan

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ABSTRACT.—Photosynthetic gas exchange was measured *in situ* with either the adaxial or abaxial leaf surface illuminated on vertical, horizontal, and angled leaves of *Asplenium nidus* and vertical leaves of *Ophioderma pendula*, two epiphytic ferns in a subtropical rain forest in northeastern Taiwan. Leaves for gas exchange measurements were selected to ensure a diversity of different exposures of the two leaf surfaces to direct sunlight. For most leaves of both species, photosynthetic rates were higher when the side of the leaf that typically received more direct insolation was illuminated during the gas exchange measurement. Higher rates of net CO_2 uptake when one side of the leaf was illuminated, relative to rates when the opposite side was illuminated, were attributable to a greater biochemical capacity for photosynthesis, not to greater stomatal conductances. Based on the results of this study, the photosynthetic capacity of the two sides of the leaves of epiphytic ferns, for the most part, reflects the degree of exposure of each side of the leaf to direct sunlight, as has been found in similar studies of terrestrial taxa.

KEY WORDS.—abaxial leaf surface, adaxial leaf surface, *Asplenium*, epiphytes, illumination, leaf angle, *Ophioderma*, photosynthesis, subtropical forest, Taiwan

Most leaves are green and, thus, presumably capable of some level of photosynthetic activity, even if just recycling respiratory CO_2, on both their adaxial and abaxial surfaces (Moore *et al.*, 1998; Terashima, 1986). Work with terrestrial taxa has shown that the capacity for photosynthesis is equal, or nearly so, when either leaf surface of vertically oriented leaves is illuminated, as long as both surfaces intercept similar amounts of solar radiation during leaf development (Syvertsen and Cunningham, 1979; DeLucia *et al.*, 1991; Poulson and DeLucia, 1993). In contrast, if one side of a vertically oriented leaf typically receives more insolation than the opposite side, the photosynthetic capacity of the leaf is greater when the normally sunlit surface is irradiated during photosynthetic measurements, relative to photosynthesis when the shaded side is irradiated (Poulson and DeLucia, 1993; but see Václavík, 1984)

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Likewise, the photosynthetic activity of horizontally oriented leaves is greater when their adaxial surface is illuminated than when their abaxial surface is illuminated (Syvertson and Cunningham, 1979; Terashima, 1986; DeLucia *et al.*, 1991) The latter applies only to the sun leaves, not the shade leaves, of Sitka spruce (Leverenz and Jarvis, 1979).

Epiphytic vascular plants appear to have been excluded from such studies, yet are ideal subjects for such investigations. Epiphytic vascular plants often exhibit a great diversity of leaf orientations and exposures (Benzing, 1990). For example, epiphytes with a rosette growth form often have leaves ranging from vertical to horizontal, and many have intermediate angles. Furthermore, a number of epiphytic taxa have vertically oriented leaves that are, unlike their terrestrial counterparts, positively geotropic. Most epiphytes also live in a complex light environment, being shaded by the host tree stem and canopy, as well as surrounding trees, depending on the location of the sun at any point in time. Given their leaf angles and the complexity of the light environment in which epiphytes grow, it is difficult to predict how the photosynthetic capacity of the two sides of the leaves of such plants compare and whether or not findings based on terrestrial taxa might apply to epiphytes. Therefore, the goal of this study was to determine if photosynthesis in epiphytes, particularly ferns, responds to leaf surface illumination in a similar manner as has been found in terrestrial plants.

Materials and Methods

Study site and species.—Leaf photosynthetic parameters were measured for six individuals of *Asplenium nidus* L. and five individuals of *Ophioderma pendula* (L.) Presl *in situ* at the Fushan Experimental Forest, a comparatively pristine tract of subtropical rainforest (121°34′E, 24°46′N) at an elevation of ~600 m located 40 km southeast of Taipei in northeastern Taiwan. For general climatic conditions at the Fushan site, see Martin *et al.* (2004). Environmental conditions during the week of measurements (11–15 July 2005) were: 25.1° C average daily air temperature (29.8° C average daily maximum; 21.3° C average daily minimum), 4.2 mbar average daily vapor pressure deficit (vpd); and 20.0 mol m^{-2} day^{-1} average daily Photosynthetic Photon Flux Density (PPFD).

Asplenium nidus and *O. pendula* were chosen for this investigation to ensure a diversity of different exposures of the two leaf surfaces to direct sunlight. Plants were selected in a partially disturbed section of the forest to allow easy access for *in situ* measurements of photosynthesis. The study site included several walking trails and was tens of meters from a laboratory building. Species of dominant trees at this site were numerous, primarily in the families Fagaceae and Lauraceae; examples include *Litsea acuminata* (Bl.) Kurata (Lauraceae), *Machilus zuihoensis* Hayata (Lauraceae), *Castanopsis cuspidata* (Thunb. *ex* Murray) Schottky var. *carlesii* (Hemsl.) Yamazaki (Fagaceae), and *Pasania hancei* (Benth.) Schottky (Fagaceae).

All plants were large (plant diameter for *A. nidus* ≥ 0.5m and leaf length for *O. pendula* ≥ 0.5m) growing epiphytically on a variety of host trees, including those listed above. Most plants had sporangia on some leaves at the time of this study (sporangia-bearing portions of the leaves were avoided in all measurements to avoid effects of sporangia on the measurements (Chiou *et al.* 2004). All leaves were measured no higher than three to four meters from the ground, i.e., within arm's reach while standing, with or without a ladder. Only mature, non-senescent leaves lacking substantial insect damage were sampled; very young and very old leaves were avoided. Leaves were selected without regard to host tree species, height from the ground (except as noted), and degree of canopy shade at the time of measurements.

Photosynthesis measurements.—Photosynthesis was measured on three different leaves for each of six plants of *A. nidus*; the three leaves were selected for measurements based primarily on the likelihood of exposure of each leaf surface to direct sunlight. Horizontal leaves were older (based on size, presence of sporangia, weathering, and phyllotaxy of the epiphyte) than the other two leaves selected for measurements and grew perpendicular to and away from the host tree trunk. Such leaves should intercept very little direct sunlight on their abaxial surface, whereas their adaxial surface should intercept direct sunlight during much of a sunny day. Angled leaves grew at about a 45 degree angle from the tree trunk, so should occasionally intercept direct sunlight on both surfaces of the leaf. Vertical leaves grew close to the trunk of the host tree, and, thus, were shaded by the trunk much of the day. These leaves should intercept little light on their adaxial surface most of the day, but occasionally direct sunlight on their abaxial surface, depending on the location of the sun. All leaves of *Ophioderma pendula* grew with similar exposure to light on their two surfaces as in the "vertical" leaves of *A. nidus*, but, in contrast to leaves of *A. nidus*, the growth of *O. pendula* leaves was positively geotropic. Another important difference between the "vertical" leaves of these two epiphytic ferns is that the leaf sides are reversed in the two taxa, i.e., in *A. nidus*, the abaxial side of the "vertical " leaves faces outward, and is thus more exposed to solar irradiation, whereas, the adaxial surfaces of the *O. pendula* leaves face outward and are thus more exposed to direct sunlight. Although intercepted sunlight on all leaves and their two surfaces was not measured, field observations during this study confirmed the above statements.

Photosynthesis was measured with a LI-COR (Lincoln, NE) LI-6400 Portable Photosynthesis System. Because all leaves measured were large, the area of leaf for which gas exchange was measured matched the maximum area possible (6 cm^2) in the gas exchange chamber. Photosynthetic parameters were measured two different ways at the central portion of each leaf: once with the adaxial surface illuminated and again adjacent to the same leaf location with the abaxial surface illuminated. The exact same location on the leaf was not used for both measurements to ensure that manipulation by inserting the leaf into the chamber and clamping the chamber on the leaf for the first measurement did not influence the second measurement. Although gas exchange was always measured for both sides of the leaf simultaneously, the chamber was oriented such that only the adaxial or abaxial surface received light from the blue and red diodes in the top half of the chamber. Very little ambient light reached the opposing leaf surface during the measurements as a result of shading by parts of the gas exchange chamber, the investigators, and nearby vegetation. For both species, photosynthesis was measured three times with illumination on one surface of a leaf at a low PPFD (100 $\mu mol\ m^{-2}\ s^{-1}$), then three times at a high PPFD (1000 $\mu mol\ m^{-2}\ s^{-1}$). Using the same leaf, the chamber was then reversed to measure gas exchange with illumination (both PPFD levels) on the opposite leaf surface. Net CO_2 uptake in *A. nidus* saturated at approximately 500 $\mu mol\ m^{-2}\ s^{-1}$ (determined with preliminary gas exchange measurements). Other environmental conditions during all measurements were maintained by the LI-6400 system at the following values: air CO_2 concentration of 370 $\mu mol\ mol^{-1}$, chamber ("block") temperature of 30°C (leaf temperatures were typically 0.5° C higher), vapor pressure deficit (vpd) of 0.9 mbar, and flow rate of 200 $\mu mol\ s^{-1}$. Lower vpd values resulted in exceedingly low transpiration rates, which led to unrealistic values for C_i; any such data were discarded. For each gas exchange measurement, data were recorded only when gas exchange rates were stable (Coefficient of Variation of exchange rates of both gases and flow rates not varying by more than 0.2% among successive measurements every 2–3 seconds), typically within 10 seconds of inserting the leaf in the gas exchange chamber or after the previous measurement (for a total of three repeated measurements). The gas exchange chamber remained clamped to a leaf for approximately five minutes at each light level, allowing for stable readings, as well as steps taken to ensure instrument accuracy (e.g., using the "match" function of the LI-6400 prior to each measurement).

Statistical analyses.—For both species, means ($N=5$ or 6 plants; the value for each plant being a mean of three repeat measurements; see above) of abaxial and adaxial gas exchange parameters at each light level were compared with a paired Student's *t*-test when the data met the assumptions of parametric statistics (Sokal and Rohlf, 1981) or with a Mann-Whitney *U*-test otherwise.

Results and Discussion

The adaxial side of the vertical leaves growing out of the rosettes of *A. nidus* is unlikely to receive direct radiation due to shading by the host tree trunk, whereas the exposed abaxial side should at least occasionally intercept direct solar radiation. Thus, based on results with terrestrial plants (Syvertson and Cunningham, 1979; Terashima, 1989; DeLucia *et al.* 1991; Poulson and DeLucia 1993), it was predicted that the illumination of the abaxial side of the vertical leaves of *A. nidus* would result in higher photosynthetic rates than when the adaxial side of the same leaf is illuminated. Measurements of photosynthesis at both high and low PPFD of plants in northeastern Taiwan did not, however, support this prediction (Fig. 1). In contrast, although not statistically significant (high PPFD $P= 0.28$; low PPFD $P = 0.17$), the trend in

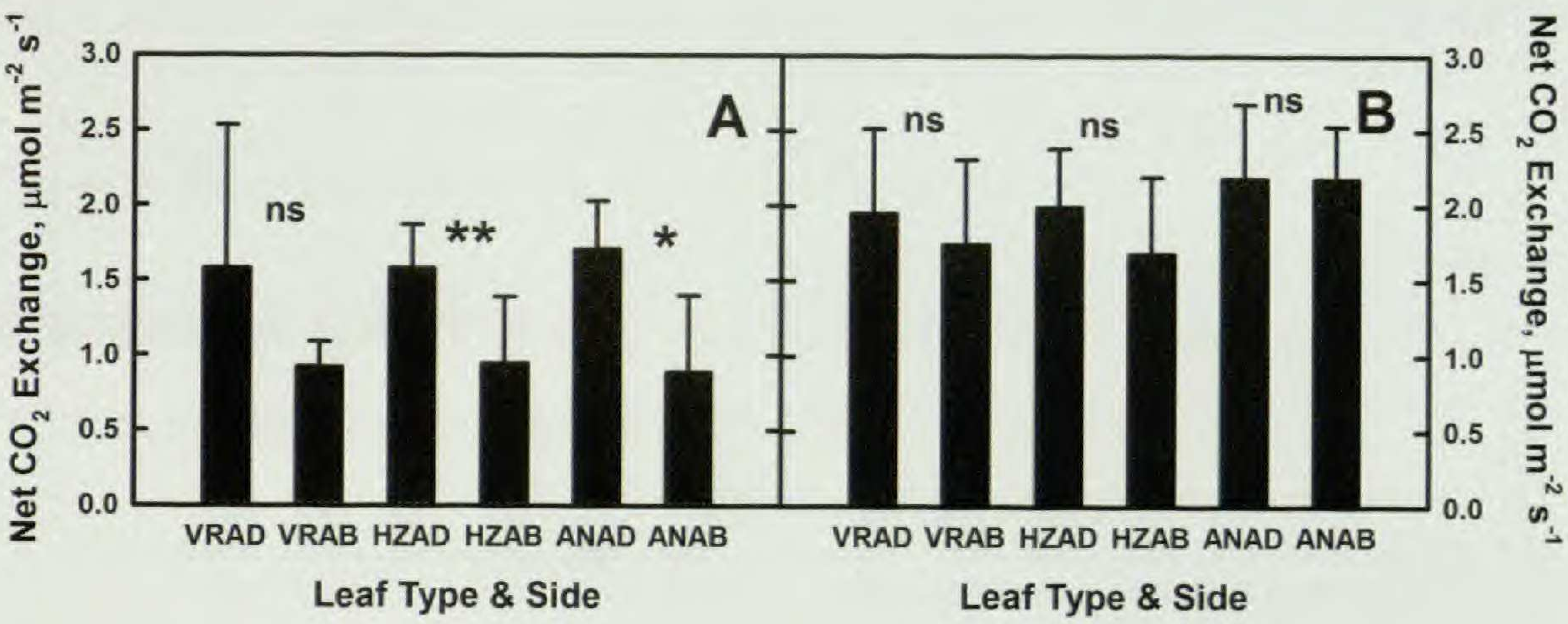

FIG. 1. Mean (lines projecting from bars are standard deviations; n = 6 plants, three repeated measurements/leaf/plant) rates of net CO_2 exchange (positive values indicate CO_2 uptake) for different leaves and with illumination at two light levels on either side of the leaves of the epiphytic fern *Asplenium nidus* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for type and side of leaf are: "VR" = vertical, "HZ" = horizontal, "AN" = angled (45° from vertical); and "AD" indicates illumination (A, 100 μmol m^{-2} s^{-1}; B, 1000 μmol m^{-2} s^{-1}) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. The abaxial and adaxial means for two leaves at low PPFD are significantly different at $P < 0.05$ or $P < 0.01$ indicated by "*" or "**", respectively, above each pair of means, while the other pairs of means are not significantly different ($P > 0.05$, indicated by "ns" above each pair of means).

the data indicated the opposite of expectations, i.e., photosynthetic rates at either PPFD appeared higher when the adaxial surface was illuminated. According to the statistical analyses, however, photosynthetic rates at both light levels were equal regardless of which side of the leaf was illuminated (Fig. 1).

Light interception of the two surfaces of the horizontal leaves of the epiphytic fern *A. nidus* is quite different from that of the vertical leaves, and the prediction of comparative photosynthetic capacities when the two sides of this leaf are illuminated is the opposite of that of the vertical leaves of this fern. Because the adaxial surfaces of these leaves intercept more direct solar radiation than do the abaxial surfaces, photosynthetic rates when the adaxial surface of the horizontal leaves of this epiphyte are illuminated should be higher than those of the leaf when the abaxial surface of the same leaf is illuminated. Measurements of photosynthetic rates confirmed this prediction, although the higher photosynthetic rates when the adaxial side of the leaves was illuminated were statistically significant only when measurements were made at the lower PPFD (Fig. 1). These higher net CO_2 uptake rates were accompanied by equal transpiration rates (Fig. 2) and stomatal conductances (Fig. 3), while internal CO_2 concentrations were significantly lower (Fig. 4) These gas exchange results indicate that the higher photosynthetic rate was most likely the result of a greater biochemical capacity for photosynthesis and not the result of greater stomatal opening and, hence, easier gas diffusion into

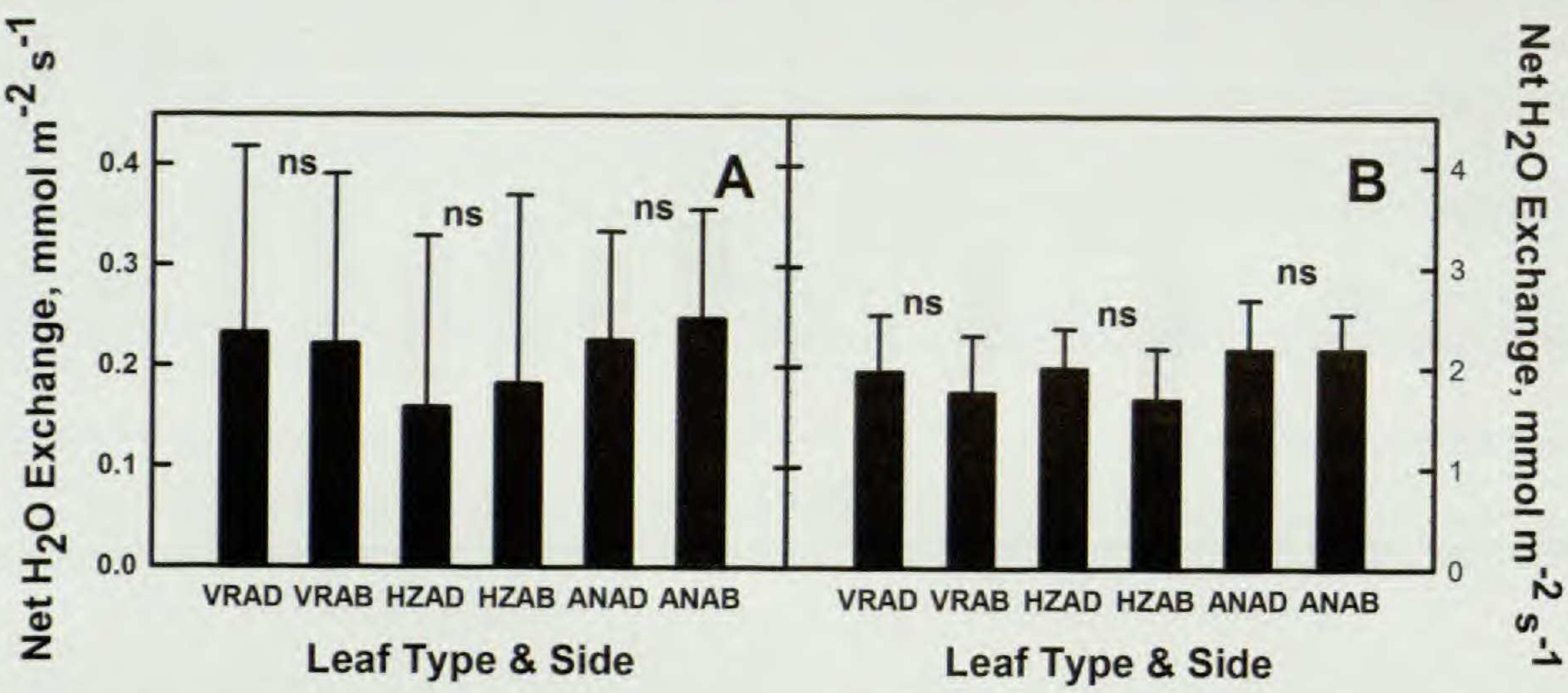

FIG. 2. Mean (lines projecting from bars are standard deviations; n = 6 plants, three repeated measurements/leaf/plant) rates of net H_2O exchange (positive values indicate water vapor loss) for different leaves and with illumination at two light levels on either side of the leaves of the epiphytic fern *Asplenium nidus* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for type and side of leaf are: "VR" = vertical, "HZ" = horizontal, "AN" = angled (45° from vertical); and "AD" indicates illumination (A, 100 μmol m^{-2} s^{-1}; B, 1000 μmol m^{-2} s^{-1}) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. None of the abaxial and adaxial means at any leaf location are significantly different ($P > 0.05$, indicated by "ns" above each pair of means).

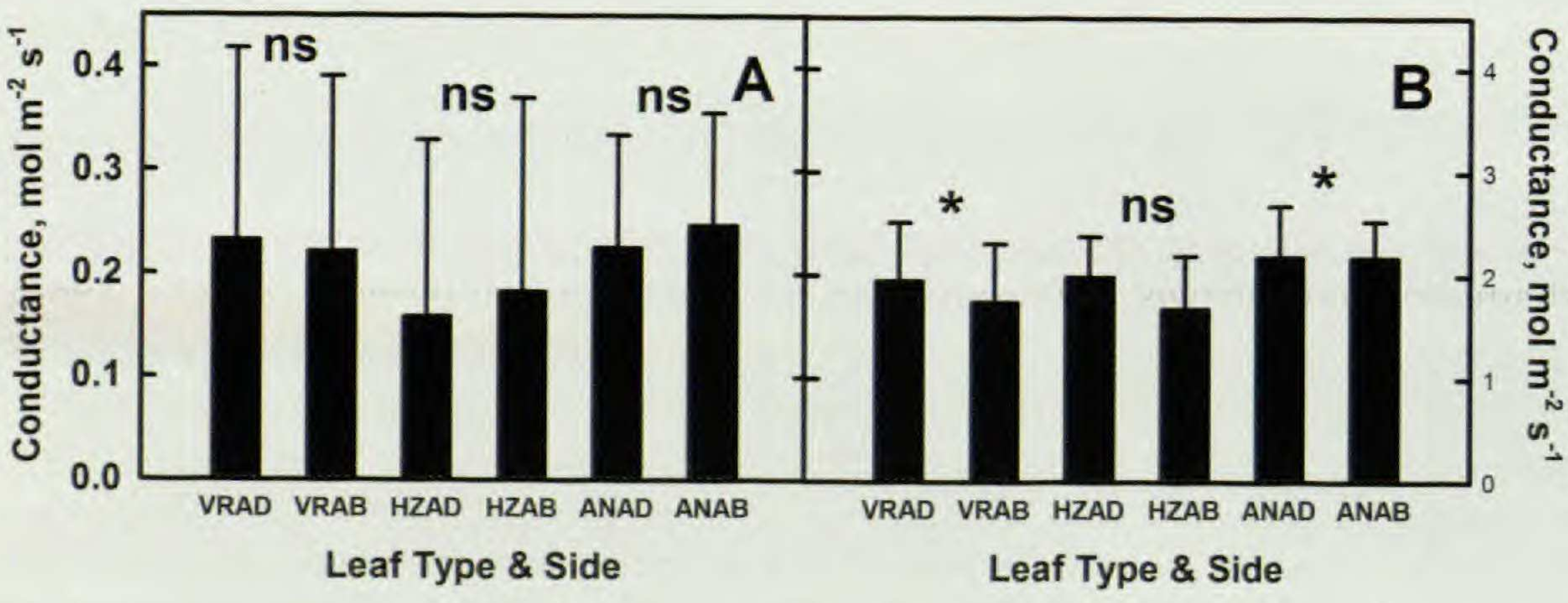

FIG. 3. Mean (lines projecting from bars are standard deviations; N = 6 plants, three repeated measurements/leaf/plant) stomatal conductances for different leaves and with illumination at two light levels on either side of the leaves of the epiphytic fern *Asplenium nidus* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for type and side of leaf are: "VR" = vertical, "HZ" = horizontal, "AN" = angled (45° from vertical); and "AD" indicates illumination (A, 100 μmol m^{-2} s^{-1}; B, 1000 μmol m^{-2} s^{-1}) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. The abaxial and adaxial means at two leaf locations at high PPFD are significantly different at $P < 0.05$, indicated by "*" above each pair of means, while the other pairs of means are not significantly different ($P > 0.05$, indicated by "ns" above each pair of means).

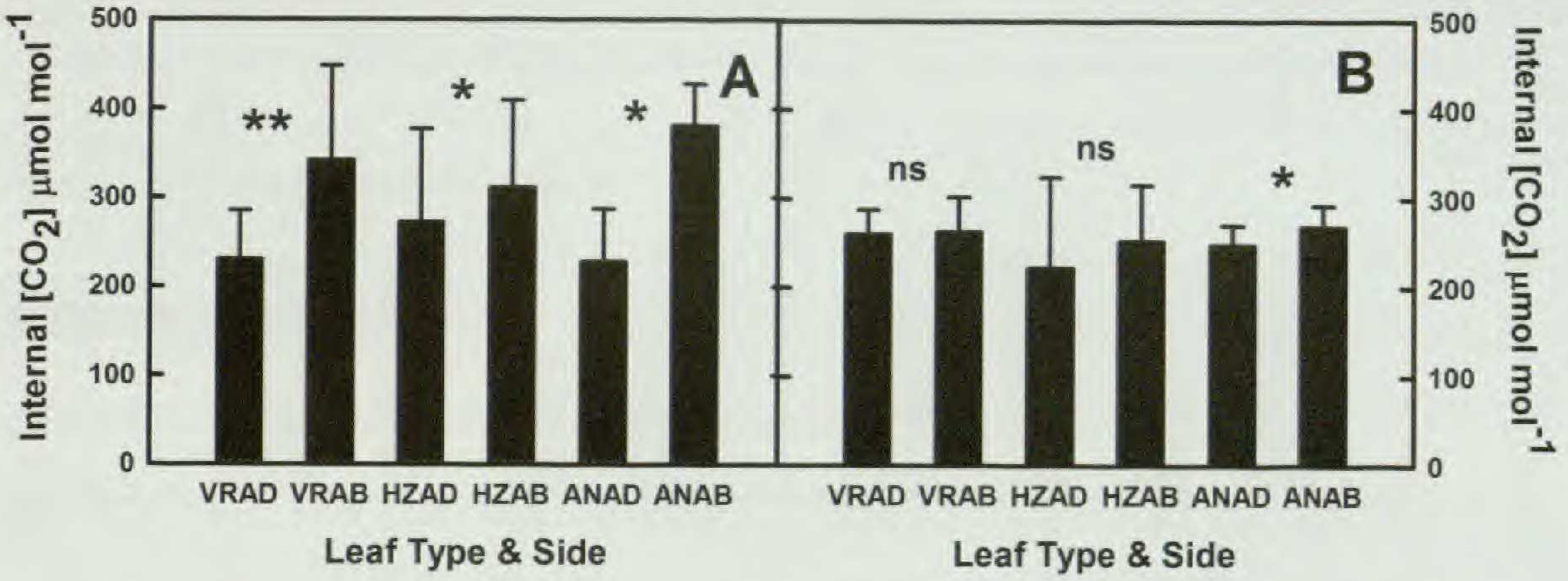

FIG. 4. Mean (lines projecting from bars are standard deviations; N = 6 plants, three repeated measurements/leaf/plant) leaf internal CO_2 concentrations (external CO_2 concentration was 370 $\mu mol\ mol^{-1}$) for different leaves and with illumination at two light levels on either side of the leaves of the epiphytic fern *Asplenium nidus* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for type and side of leaf are: "VR" = vertical, "HZ" = horizontal, "AN" = angled (45° from vertical); and "AD" indicates illumination (A, 100 $\mu mol\ m^{-2}\ s^{-1}$; B, 1000 $\mu mol\ m^{-2}\ s^{-1}$) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. The abaxial and adaxial means at several leaf locations are significantly different at $P < 0.05$ or $P < 0.01$, indicated by "*" or "**", respectively, above each pair of means, while the other pairs of means are not significantly different ($P > 0.05$, indicated by "ns" above each pair of means).

the leaf (Farquhar and Sharkey, 1982; Sharkey, 1985). In agreement with the latter interpretation, it is possible, especially for the measurements made at high light, that illumination of the abaxial surface resulted in photoinhibition in this lateral half of the section of leaf being measured. This possibility is supported by previous findings that the side of a leaf that is typically less exposed to sunlight has chloroplasts and photosynthetic features typical of shade-adapted leaves (Schreiber *et al.*, 1977; Kulandaivelu *et al.*, 1983; Terashima and Inoue, 1984; Terashima *et al.*, 1986). Differences in photosynthetic capacity depending on which side of the leaf is illuminated might also reflect other anatomical or optical (e.g., absorptance) features of the two sides of the leaf (Terashima 1986; DeLucia *et al.*, 1991). Such differences would also be interpreted as non-stomatal and non-diffusional mechanisms responsible for differences in photosynthesis between the two sides of the leaf, as was found in this study.

Both the adaxial and abaxial surfaces of the "angled" leaves of *A. nidus* should intercept direct sunlight, at least for brief periods, throughout a day. Thus, one might predict that the photosynthetic capacity of these leaves is comparable, regardless which surface is illuminated (Syvertsen and Cunningham, 1979; Václavík, 1984; DeLucia *et al.*, 1991; Poulson and DeLucia, 1993). Based on measurements made *in situ* with this epiphytic fern in northeastern Taiwan, this prediction was supported when gas exchange was measured at high PPFD (Fig. 1), but the photosynthetic rate when the adaxial leaf surface

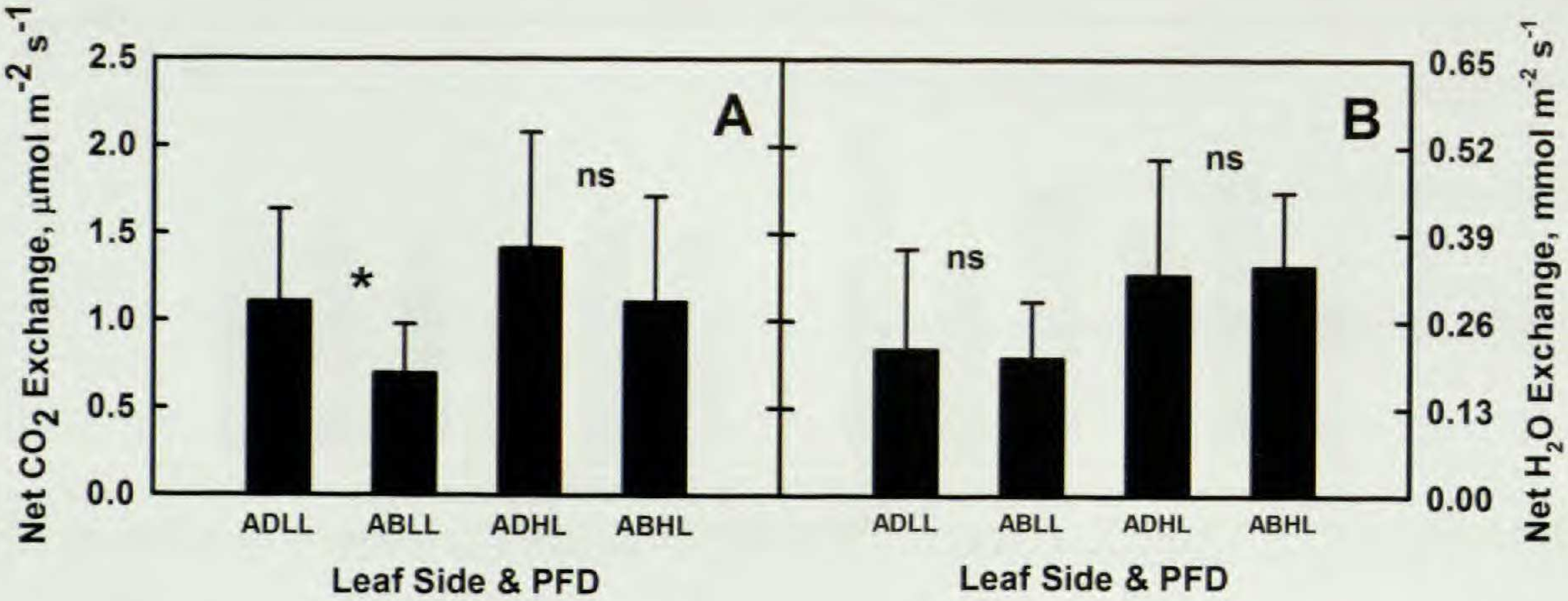

FIG. 5. Mean (lines projecting from bars are standard deviations; n = 5 plants, three repeated measurements/leaf/plant) rates of net CO_2 exchange (A; positive values indicate CO_2 uptake) and rates of net water vapor exchange (B; positive values indicate water vapor loss) with illumination at two light levels on either side of the leaves of the epiphytic fern *Ophioglossum pendula* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for side of leaf and light level are: "AD" indicates illumination (LL = 100 μmol m^{-2} s^{-1}; HL= 1000 μmol m^{-2} s^{-1}) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. The abaxial and adaxial means at high PPFD are significantly different at $P < 0.01$, indicated by "*" above that pair of means, while the other pairs of means are not significantly different ($P > 0.05$, indicated by "ns" above that pair of means).

was illuminated exceeded that when the abaxial surface of the leaf was illuminated at low PPFD (Fig. 1). As was the case with the horizontal leaves, the higher net CO_2 exchange rate of the angled leaves was apparently the result of a greater biochemical capacity for photosynthesis, generating a lower leaf internal CO_2 concentration (Fig. 4), and not due to a greater stomatal conductance (Fig. 3; Farquhar and Sharkey, 1982; Sharkey, 1985). These findings contrast directly with those for Sitka spruce by Leverenz and Jarvis (1979), who found that differences in photosynthetic capacity of the leaves, depending on which side of the leaf was illuminated could be ascribed to differences in stomatal conductance, not to the biochemical capacity of the leaf.

The leaves of *Ophioderma pendula* are positively geotropic, hanging vertically from the main body of this epiphytic fern and remaining close to the main stem of the host tree. As a result of shading by the immediately adjacent host tree trunk, the abaxial surfaces of these leaves seldom receive direct solar radiation. Thus, it was predicted that photosynthetic rates, at least at the higher PPFD, when the adaxial surface of these leaves is illuminated, would exceed those when the abaxial surfaces of these leaves are illuminated for plants measured *in situ* in this subtropical rain forest. This was indeed the case for net CO_2 exchange measurements at both high and low PPFD (Fig. 5). Because rates of transpiration and stomatal conductances were equal when either side of the leaves was illuminated during gas exchange measurements

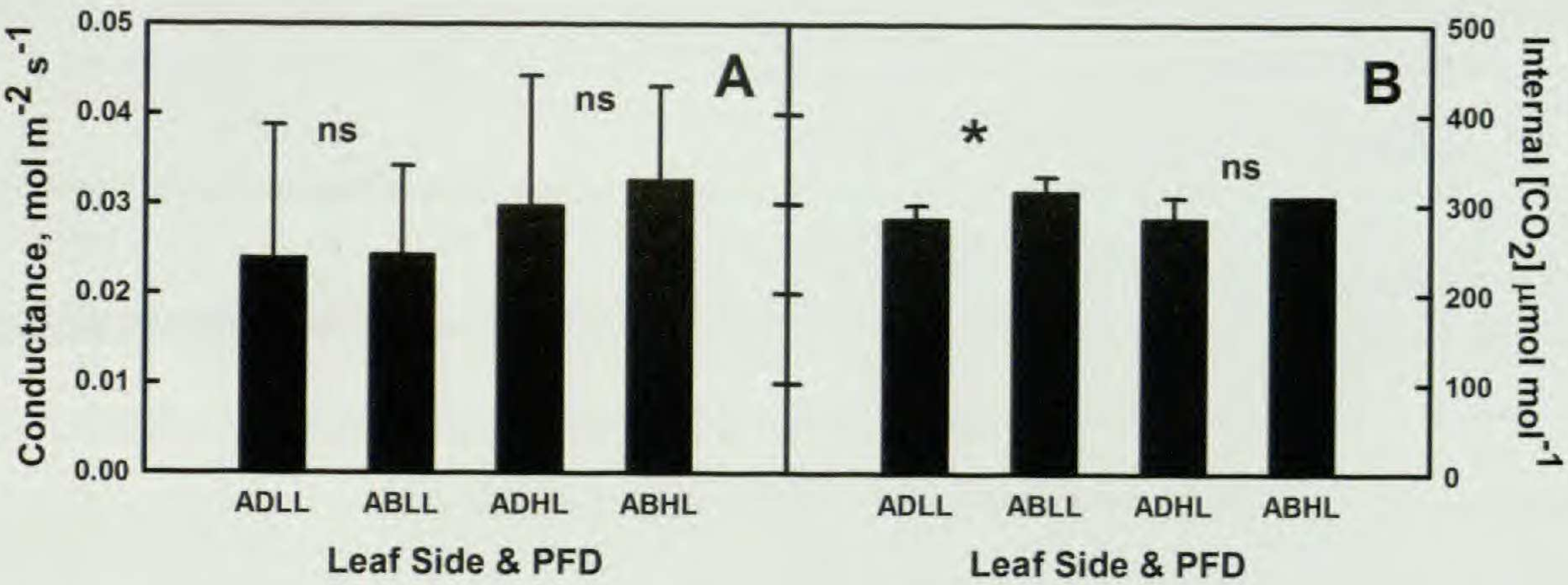

FIG. 6. Mean (lines projecting from bars are standard deviations; n = 5 plants, three repeated measurements/leaf/plant) stomatal conductances (A) and leaf internal CO_2 concentrations (B; external CO_2 concentration was 370 μmol mol^{-1}) with illumination at two light levels on either side of the leaves of the epiphytic fern *Ophioglossum pendula* measured *in situ* in a subtropical rain forest in northeastern Taiwan). Abbreviations for side of leaf and light level are: "AD" indicates illumination (LL = 100 μmol m^{-2} s^{-1}; HL= 1000 μmol m^{-2} s^{-1}) provided to the adaxial side of the leaf during gas exchange measurements; "AB" indicates illumination (low and high PPFD as in AD) provided to the abaxial side of the leaf during measurements. Neither pair of abaxial and adaxial means is significantly different ($P > 0.05$, indicated by "ns" above the pairs of means).

(Figs. 5, 6), and because internal CO_2 concentrations were lower (although not statistically significantly so at high PPFD; Fig. 6) when the adaxial surface was illuminated, the mechanism underlying the higher rate of net CO_2 uptake when the adaxial surface was illuminated appears, as was the case in several instances with *A. nidus*, to reflect a greater biochemical capacity for photosynthesis, not a greater stomatal conductance allowing easier CO_2 diffusion into the leaf (Farquhar and Sharkey, 1982; Sharkey, 1985).

Overall, the results of *in situ* gas exchange measurements with two epiphytic ferns in a subtropical rain forest in northeastern Taiwan lend considerable, but not complete, support to past findings with terrestrial taxa (Syvertsen and Cunningham, 1979; Terashima, 1989; DeLucia *et al.*, 1991; Poulson and DeLucia, 1993). In most, but not all, cases, if a leaf is oriented such that one side receives more direct solar radiation than the other, the leaf has a higher photosynthetic capacity when the more exposed surface is illuminated. In addition, this higher capacity reflects a greater biochemical capacity for photosynthesis and not easier diffusion of CO_2 into the leaf (Farquhar and Sharkey 1982; Sharkey, 1985).

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